

Atmospheric Water Absorption and the Water Budget of Terrestrial Isopods (Crustacea, Isopoda, Oniscidea)

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Abstract. Studies of terrestrial isopods (Crustacea, Isopoda, Oniscidea) have revealed a capacity for active water vapor absorption (WVA) in the taxonomic sections Crinocheta and Diplocheta but not in Synocheta. Uptake thresholds in Crinocheta are modest by comparison with other vapor absorbers, but standardized uptake fluxes are among the highest recorded and are probably an adaptive requirement to counter the high transpiratory losses. Comparative data for uptake fluxes, thresholds, and transpiratory losses allows the compilation of water budgets in hypothetical temperature and humidity regimes. Given a 12-h light-dark cycle, with saturated ambient activities for diurnal WVA, all species could recover water losses incurred during nocturnal foraging in an ambient water activity of 0.75, and xeric species could forage in activities below 0.30. Xeric trends based on these models agree closely with predictions from ecotypic surveys. In the littoral *Ligia oceanica* (Diplocheta) haemolymph hyperosmosis and periodic submergence provide additional means of water balance regulation. It is proposed that WVA in *Ligia* provides an essentially solute-free water source to counteract salt-loading in the splash-zone. The absence of WVA in synochetes, together with their cryptozoic habits, reflects an alternative terrestrial strategy to those of other oniscideans.

Introduction

Atmospheric water vapor absorption (WVA) is an active process enabling certain terrestrial organisms to exploit a physical state of water which is often spatially and temporally more abundant than liquid sources. A capacity for WVA has been described in several insect groups: lep-

ismatid Thysanura (Noble-Nesbitt, 1970; Okasha, 1972); Blattodea (Edney, 1966; O'Donnell, 1977, 1981, 1982); Siphonaptera (Knulle, 1967; Rudolph and Knulle, 1982); Psocoptera and Mallophaga (Knulle and Spadafora, 1969; Rudolph, 1982a, b, 1983); tenebrionid larvae (Mellanby, 1932; Ramsay, 1964; Grimstone *et al.*, 1968; Machin, 1975); and lepidopteran larvae (Chauvin and Vannier, 1980). Other major exponents of vapor absorption include certain acarine families (Lees, 1946; Rudolph and Knulle, 1979; Knulle and Rudolph, 1982). Recently, WVA has been demonstrated in the oniscidean isopods (Wright and Machin, 1990), the only crustaceans having attained major ecotypic diversification on land. Adaptations for WVA have yet to be demonstrated in myriapods and the non-acarine arachnids. There is one described case of vapor absorption in a desert plant *Nolana mollis*, a succulent shrub from the Atacama (Mooney *et al.*, 1980).

Our understanding of the physiological processes involved in vapor absorption is fragmentary. Any mechanism does, however, have basic prerequisites. A water-collecting surface must be brought into contact with the humid air and must contain fluids of depressed water vapor pressure, and hence depressed water activity (= relative humidity/100) such that water vapor moves thermodynamically into the collecting fluid. The collected fluid must then be moved internally, by imbibition or co-transport with solutes. The minimum water activity (a_w) generated by the collecting fluid constitutes the minimum activity of water vapor, or ambient activity (Aa_w), from which absorption is possible, defined as the uptake threshold (Machin, 1979a). The activity at which vapor absorption balances passive losses is referred to as the critical equilibrium activity or CEA (after Knulle and Wharton, 1964); a net gain in water is thus possible in ambient activities above the CEA. Physical principles of vapor-liquid transitions and energetic considerations are dis-

cussed by Wharton and Richards (1978), Machin (1979a), and O'Donnell and Machin (1988).

Vapor absorption systems based on colligative lowering of vapor-pressure require a compartment, isolated from the haemolymph, in which solutes can be accumulated by active transport. Hyperosmotic fluids have been identified in the cryptonephridial systems of tenebrionid larvae (Ramsay, 1964; Machin, 1979b; O'Donnell and Machin, 1991; Machin and O'Donnell, 1991), creating an activity gradient between the rectal lumen and the peripheral Malpighian tubules. They have also recently been described in the salivary secretions of ticks (Sigal *et al.*, 1991), although conflicting data is presented by Gaede (1989). Deeply folded apical and basal membranes with densely packed mitochondria suggest ion transport compatible with production/resorption of hyperosmotic fluids in the recta of flea larvae (Bernotat-Dalielowski and Knulle, 1986) and thysanurans (Noirot and Noirot-Timothee, 1971).

The hypopharyngeal bladders of the desert cockroach *Arenivaga* appear to exploit a different absorption mechanism (O'Donnell, 1981, 1982). The bladders are covered in hydrophilic hairs which are moistened by the cyclical secretion of a fluid comparable in ionic strength to the haemolymph. It is proposed that, by altering the iso-electric point of the cuticular chitin and/or protein, this fluid reduces water affinity and the hairs release water which is subsequently imbibed. Condensation onto the bladder surfaces reverses the trend, decreasing the ionic concentration of the remaining frontal body fluid, and increasing the water affinity of the cutaneous hairs. The process is thus self-sustaining and the hairs absorb water until it is released by the next pulse of uptake fluid. A similar mechanism may operate in the Psocoptera and Mallophaga, based on alterations in the iso-electric point of protein polymers secreted onto the lingual sclerites (Rudolph, 1982b, 1983; O'Donnell and Machin, 1988).

Blocking experiments have established that vapor uptake in oniscidean isopods occurs in the pleon with water possibly being absorbed across the pleopodal endopods (Wright and Machin, 1990; Wright and Machin, 1993). Prior to absorption, a strongly hyperosmotic fluid consisting mostly of Na^+ and Cl^- is secreted into the 'pleo-ventralraum' (PV) (Wright and O'Donnell, 1992), the cavity formed between the imbricate pleopodal exopods and the pleon sternites. A few minutes later, the pleopods begin a metachronal ventilatory rhythm and the fluid volume declines. There is a simultaneous drop in the fluid osmolality such that its vapor pressure increases to levels only slightly below that of the ambient air (Wright and O'Donnell, 1992). Since pleopodal ventilation is invariably associated with WVA in gravimetric studies, and has only otherwise been observed during maxillary urination, the dilution of uptake fluid is attributed to the onset of

vapor condensation. Pleopodal ventilation presumably functions to circulate air over the uptake fluid and may be involved in fluid transport and dissemination.

This explanation for the absorption mechanism requires modification at vapor activities close to the uptake threshold. Under these conditions, pleon fluid osmolalities will sometimes equate with water vapor pressures above those of the ambient air, and are thus incompatible with uptake by direct condensation. It has been proposed (Wright and O'Donnell, 1992) that cyclical compression of air within the PV serves to increase the vapor density and hence increase water activity above that of the uptake fluid. Intermittent compression of air during pleopodal ventilations is suggested by visible pulses of displaced fluid at the pleopodal margins. Such 'pressure cycling' has subsequently been confirmed by monitoring pressure changes coincident with pleopodal ventilations (Wright and Machin, 1993). Interventions of pressure cycling are also detectable gravimetrically as sharp deviations from the typical linear uptake kinetics when net flux is plotted against $A_{a,w}$. Such plots indicate that the pressure changes involved are relatively small: 3.65–6.38 kPa for seven common, temperate Crinocheta. It provides a supplement to the usual colligative absorption mechanism, allowing animals to boost uptake in near-threshold activities. The feasibility of pressure cycling as a means of water recovery was first noted by Maddrell (1971). It has subsequently been suggested as a widespread means of water conservation in insect tracheal systems, and to play a role in the vapor absorption mechanism of lepismatids and siphonapterans (Corbet, 1988).

The described uptake thresholds for oniscideans are approximately $a_w = 0.90$ (Wright and Machin, 1990), modest by comparison with many other vapor absorbers. The pyroglyphid dust mite *Dermatophagoides farinae* Hughes, for example, has a critical equilibrium activity 0.70 (Arlan and Wharton, 1974). Psocoptera and Mallophaga display uptake thresholds below 0.50 (Rudolph, 1982a, b, 1983) and respective thresholds of 0.45 and 0.43 have been demonstrated for *Thermobia* (Lepismatidae) (Noble-Nesbitt, 1969) and larvae of *Lasioderma* (Anobiidae) (Knulle and Spadafora, 1970). Uptake fluids based on the major cellular electrolytes (Na^+ , K^+ , Cl^-) are limited in colligative vapor pressure lowering by saturation: NaCl saturates at an activity of 0.75 and KCl at 0.85 (Winston and Bates, 1960). However, it has been proposed that larvae of the tenebrionid *Onymacris plana* exploit supersaturation of KCl to depress the threshold down to 0.81 (Machin and O'Donnell, 1991). Avoidance of crystallization may depend on 'supersaturation proteins' which bind to crystal surfaces, presenting conformations incompatible with crystal growth. Analogous 'antifreeze proteins' are widely documented in freeze-resistant or-

ganisms and serve to block the growth of ice crystals during supercooling (Davies and Hew, 1990).

Uptake thresholds and absorption kinetics are clearly the main factors determining the physiological and ecological significance of WVA in different groups. Together, these determine the humidity range over which absorption is possible and the water deficits which can be recovered in a given time. The ecological significance of equilibrium humidities in arthropods has been discussed by Knulle and Wharton (1964), with particular reference to acarines. The new finding of WVA in oniscideans is particularly interesting in this regard since, unlike other documented vapor absorbers, oniscideans are typically mesic-hygic arthropods, usually considered poorly adapted to xeric habitats (Cloudsley-Thompson, 1956; Edney, 1968). Here we report results of a comparative study of thresholds and uptake kinetics in the Oniscidea. Such information serves both to establish the range of vapor-absorbing abilities across the sub-order, and to provide a means for assessing ecotypic consequences of WVA.

Materials and Methods

Oniscideans were collected from diverse localities in England and Ontario and maintained in laboratory cultures with deciduous litter. Moistened paper towels served to regulate the culture humidities between 95% and 98% and provided a locally saturated microclimate. The following species were selected for study:

Section Crinocheta

- Oniscus asellus* Linnaeus, 1758
- Philoscia muscorum* (Scopoli, 1763)
- Armadillidium vulgare* (Latreille, 1804)
- Eluma purpurascens* Budde-Lund, 1885
- Cylisticus convexus* (De Geer, 1778)
- Porcellio dilatatus* Brandt, 1833
- Porcellio laevis* Latreille, 1804
- Porcellio scaber* Latreille, 1804
- Porcellio spinicornis* Say, 1818
- Porcellionides pruinosus* (Brandt, 1833)
- Trachelipus rathkei* (Brandt, 1833)

Section Synocheta

- Androniscus dentiger* Verhoeff, 1908
- Haplophthalmus danicus* Budde-Lund, 1880
- Trichoniscus pusillus* Brandt, 1833

Section Diplocheta

- Ligia oceanica* (Linnaeus, 1767)

The littoral species *Ligia oceanica* was maintained in an aerated tank of artificial seawater (Marine Enterprises Inc., Baltimore, MD) and fed on *Enteromorpha* sp. Emergent rocks allowed animals to move freely between air and water.

Water vapor absorption was determined gravimetrically by monitoring mass-changes of isopods in different water activities. Individual animals were contained within 10 mm × 25 mm cylindrical cages constructed from 1 mm or 2 mm mesh aluminum gauze. They were weighed in a moving air stream (1 cm s⁻¹) in a continuous-recording Sartorius 4410 digital microbalance (Sartorius GmbH, Gottingen) sensitive to 10 μg. The balance and weighing chambers were enclosed in temperature-regulated water jackets permitting accurate control of temperature and humidity of the air stream. These parameters were regulated by means of a Hewlett-Packard 71B computer and 3421A data-acquisition unit; details are given in Machin (1976). All experiments were conducted at 20.0°C.

Determinations of net flux in different ambient activities permitted the quantification of passive losses and uptake fluxes during WVA. Passive fluxes were standardized for surface area assuming the formula of Edney (1977):

$$\text{Surface area (cm}^2\text{)} = 12 \text{ Mass (grams)}^{0.67}$$

Uptake fluxes were standardized for surface area assuming a net pleoventral absorbing area of 0.05 cm² for a 100 mg animal (Wright and Machin, 1993). The net surface area of such an animal computes at 2.57 cm², so we may assume the pleoventral area to comprise a proportional area of 0.05/2.57 = 0.0195. Incorporating this factor into Edney's equation gives:

$$\text{Pleoventral area for WVA} = 0.234 M^{0.67}$$

Fluxes were also standardized for vapor pressure difference between ambient air and haemolymph. For passive fluxes, this assumed a haemolymph osmolality of 700 mosmol l⁻¹ for Crinocheta and Synocheta (Little, 1983; J. C. Wright, unpub. data) and 1157 mosmol l⁻¹ for *Ligia oceanica* (Parry, 1953). Since water activity is approximately equal to solvent mole fraction (as follows from Raoult's Law) and the molar concentration of liquid water at 20.0°C is 55.5 mol l⁻¹, the haemolymph water activity for Crinocheta and Synocheta is given as:

$$55.5/[55.5 + 0.700] = 0.988$$

Multiplying this value by the saturation vapor pressure of water at 20.0°C (2339 Pa) gives the haemolymph vapor pressure in Pascals.

For uptake fluxes, standardization was based on the absorption threshold activities for each species, and thus assumed initial secretion of uptake fluid at this activity. Justifications for this analysis are discussed in a separate paper (Wright and Machin, 1993). Unless otherwise mentioned, the term 'standardized flux' indicates flux standardized for both area and vapor pressure difference (*i.e.*, μg h⁻¹ cm⁻² Pa⁻¹).

Results

Oniscideans display considerable variation in their ability to restrict passive water losses. Since there are multiple components to water losses in this group (Lindqvist, 1971; Hadley and Quinlan, 1984; Wright and Machin, unpub. data), cumulative mass losses over time do not strictly reflect cutaneous transpiration. However, with continuous gravimetric monitoring it is possible to identify and exclude the irregular bouts of maxillary urination (Wright *et al.*, in prep.). Losses from the moist pleopodal endopods can be estimated using blocking techniques and account for less than 5% of total losses in all species investigated (Hadley and Quinlan, 1984; Wright and Machin, unpub. data). Whole-animal losses have also been shown, using an Al₂O₃ humidity sensor, to be in good agreement with losses measured across isolated cuticle (Hadley and Quinlan, 1984). Finally, carbon in respiratory CO₂ is a source of net mass-loss. Assuming a typical resting metabolism of 200 $\mu\text{l g}^{-1} \text{h}^{-1}$ for Crinocheta (Wieser, 1984), and a respiratory quotient of 1, the net mass-loss attributable to respiration is 3.7 $\mu\text{g h}^{-1}$ for a representative 70 mg animal. This is below 5% of measured losses for ambient activities below 0.97, and typically below 1% of losses for ambient activities below 0.85. For lower respiratory quotients, as with significant lipid metabolism, the respiratory mass-losses are negligible. Analysis of gravimetric losses can thus provide a close approximation of passive cutaneous transpiration.

Mean standardized loss fluxes are listed in Table I for the species studied. Pressure-standardized loss fluxes are also expressed as proportional losses (percent hydrated mass per hour per unit activity). Species fall broadly into three physiological categories, corresponding to the different taxonomic sections. The Synocheta and Diplocheta both reveal higher cuticle fluxes than Crinocheta but proportional losses differ markedly owing to size variation. Synocheta thus sustain approximately 50% mass-loss—equivalent to approximately 65% water-loss (lethal)—within 1 h in dry air. *Ligia oceanica* (Diplocheta), in contrast, suffers only 8.5% mass-loss in the same conditions. The Crinocheta reveal the lowest standardized fluxes with the least permeable species (*Armadillidium vulgare*, *Porcellionides pruinosus*) possessing comparable waterproofing to mesic-hygic insects (Edney, 1977). Proportional mass-losses range from 11.63% $M \text{ h}^{-1} a_w^{-1}$ (*Philoscia muscorum*) to 2.88% $M \text{ h}^{-1} a_w^{-1}$ (*A. vulgare*).

A capacity for WVA was confirmed for all representatives of the Crinocheta and for *Ligia oceanica*. This extends the number of Crinocheta for which WVA has been demonstrated to 12, and provides the first evidence of WVA in the Diplocheta. Despite repeated studies with both continuous and intermittent weighing, it has not been possible to identify vapor absorption in the Synocheta.

Table I

Mean masses and integumental water fluxes of Oniscidea

Species	Mean M (mg)	n	Standardized flux ($\mu\text{g h}^{-1} \text{cm}^{-2} \text{Pa}^{-1}$)	SE	Proportional flux (% $M \text{ h}^{-1} a_w^{-1}$)
Diplocheta					
<i>L. oceanica</i>	162.76	7	1.664	0.084	8.512
Synocheta					
<i>I. dentiger</i>	2.23	4	2.862	0.062	59.39
<i>H. danicus</i>	1.18	9	1.529	0.085	43.93
<i>F. pusillus</i>	2.85	10	2.929	0.229	56.86
Crinocheta					
<i>A. vulgare</i>	112.08	23	0.491	0.035	2.879
<i>C. convexus</i>	58.69	3	1.555	0.139	11.107
<i>E. purpurascens</i>	24.9	1	1.067	—	10.112
<i>O. asellus</i>	78.18	7	1.477	0.088	9.566
<i>P. muscorum</i>	16.5	2	1.069	0.111	11.63
<i>P. dilatatus</i>	89.25	3	0.800	0.034	4.670
<i>P. laevis</i>	55.25	2	0.740	0.035	5.389
<i>P. scaber</i>	54.35	10	0.719	0.075	5.694
<i>P. spunicornis</i>	42.17	18	0.690	0.066	5.733
<i>Ps. pruinosus</i>	26.89	8	0.581	0.037	5.677
<i>T. rathkei</i>	45.11	11	0.901	0.064	7.202

Data were gathered from sections of Diplocheta, Synocheta, and Crinocheta measured at 20°C. Integumental fluxes are expressed as 'standardized flux' ($\mu\text{g h}^{-1} \text{cm}^{-2} \text{Pa}^{-1}$) and as 'proportional flux'—the percentage of the hydrated mass lost per hour per unit activity deficit between haemolymph and ambient.

All species studied died within 24 h when transferred to a 10 ml vial containing saturated K₂SO_{4(aq)} to regulate the humidity at 98.0%; animals survived long after the period required for approximate humidity equilibration (RH > 97.0% in 20–30 min) so there appears to be good evidence to discount WVA in this section.

The kinetics of WVA in Crinocheta have been described before (Wright and Machin, 1990; Wright and Machin, 1993) but a brief account is included here. The description also applies to absorption in *Ligia oceanica*. Plots of net flux against ambient activity reveal a linear curve for passive losses and a capacity for variable rates of vapor uptake above a threshold activity (Fig. 1). Maximum uptake fluxes vary with ambient activity according to approximate linear kinetics, excepting augmented fluxes in near-threshold activities attributable to pressure cycling.

Plots such as Figure 1 allow the determination of regression lines for net uptake and loss fluxes, omitting sub-maximal uptake fluxes and interventions of pressure cycling. The intersection of these curves marks the uptake threshold and the intersection of the uptake curve with the ordinate of zero net flux marks the critical equilibrium activity. Slopes ($\mu\text{g h}^{-1} a_w^{-1}$) are corrected for vapor pressure by dividing by the saturated vapor pressure of water at 20.0°C (2339 Pa). True uptake fluxes ($\mu\text{g h}^{-1}$) are obtained by subtracting the slope of the loss curve from that of the net uptake curve and can be standardized for surface area and vapor pressure in the usual way.

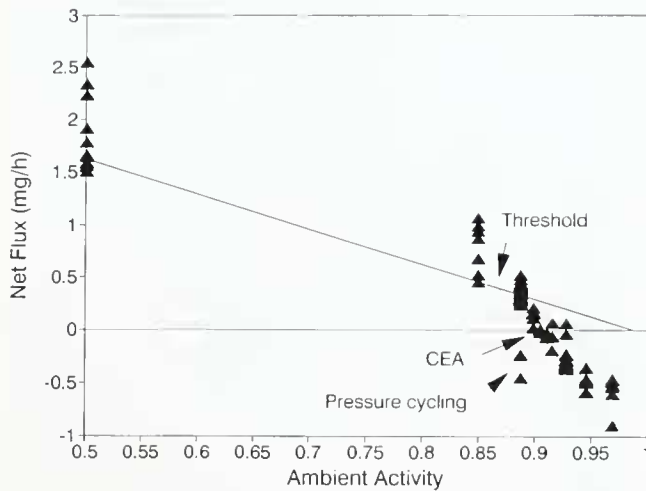


Figure 1. Example plot of net flux against ambient water activity for a vapor-absorbing oniscidean (*A. vulgare*). Each point represents the mean flux measured over a 20 or 30 min period. Passive losses (indicated as positive fluxes) decrease approximately linearly with increasing Aa_w , ceasing where this equals the haemolymph a_w (0.988). Deviations from this curve attributable to active water vapour absorption (WVA) are evident in activities above the uptake threshold, with uptake maxima showing approximate linear kinetics with Aa_w . Uptake fluxes can be modulated in any given Aa_w to balance passive losses or generate maximal uptake as required. They can also be boosted in lower activities by pressure cycling, evident in two recording periods, where compression of air within the pleoventral cavity is used to increase the activity gradient for uptake (Wright and Machin, submitted).

Uptake thresholds and critical equilibrium activities for Crinocheta and Diplocheta are listed in Table II. Species for which insufficient uptake data were available are excluded. Thresholds vary from 0.866 for *Armadillidium vulgare* to 0.927 for *Oniscus asellus*. Product-moment correlation analysis reveals a significant positive relationship between uptake thresholds and standardized loss fluxes ($P < 0.01$; Fig. 2). Species with lower uptake thresholds for WVA thus display lower integumental permeabilities, both constituting xeric adaptations. If the Crinocheta are ranked in ascending order of thresholds and CEAs, the sequence agrees closely with xeric trends based on the most comprehensive ecotypic surveys (Harding and Sutton, 1985; Sutton *et al.*, 1984).

Means and standard errors for vapor-pressure-standardized, as well as vapor-pressure and area-standardized, uptake fluxes for Crinocheta and Diplocheta are listed in Table III. This table also lists net uptake fluxes expressed as percentage of hydrated mass. Corresponding values are given for other vapor absorbers, derived from data in the literature. The most striking observation is the superior efficacy of the oniscidean uptake mechanism, with standardized uptake fluxes an order of magnitude higher than in other vapor absorbers. The Oniscidea are also among the most efficient absorbers when net uptake is expressed

Table II

Mean uptake thresholds and critical equilibrium activities for *Crinocheta* and *Diplocheta*

	Threshold	SE	CEA	n
<i>A. vulgare</i>	0.866	0.0046	0.882	5
<i>C. convexus</i>	0.905	0.0035	0.931	2
<i>P. dilatatus</i>	0.892	—	0.910	1
<i>P. scaber</i>	0.889	0.0046	0.913	5
<i>P. spunicornis</i>	0.872	0.0056	0.901	4
<i>Ps. pruinosus</i>	0.872	0.0009	0.899	3
<i>O. asellus</i>	0.927	0.0085	0.946	3
<i>T. rathkei</i>	0.893	0.0073	0.905	2
<i>L. oceanica</i>	0.900	0.0071	0.937	3

Mean uptake thresholds include standard errors.

Information was determined from vapor absorption plots such as seen in Figure 1.

per unit body mass. Since uptake flux is proportional to the area of the absorbing surface, it is expected to scale with body mass according to the relationship:

$$\text{Flux } (\mu\text{g h}^{-1} \text{Pa}^{-1}) = a \cdot \text{Mass}^{0.67}$$

Hence:

$$\text{Log Flux} = \log a + \log \text{Mass} \times 0.67$$

The log:log plot is illustrated in Figure 3 for the species listed in Table III and illustrates the superior uptake fluxes in the Oniscidea. The regression line has an x coefficient of 0.692 indicating a close fit to the predicted scaling. However, the corresponding allometric scaling for the

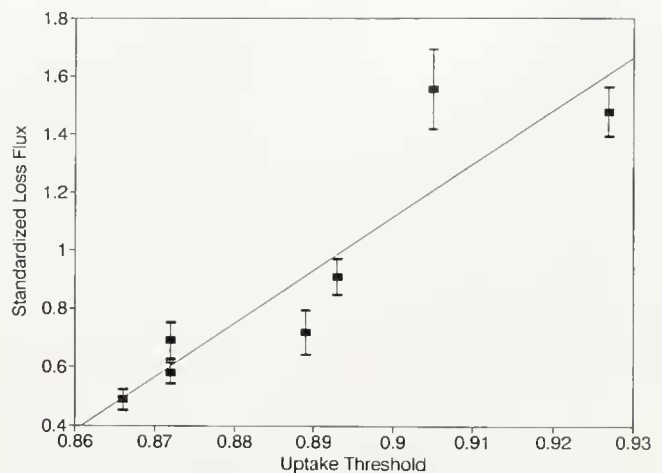


Figure 2. Plot of mean standardized loss flux ($\mu\text{g h}^{-1} \text{cm}^{-2} \text{Pa}^{-1}$) against mean uptake threshold for species of Crinocheta. Error bars are indicated for standardized flux only. The relationship reveals a significant positive correlation ($r = 0.907$, $P < 0.01$) indicating parallel selective trends towards low permeability and depressed uptake threshold in xeric species.

Table III

Inward water fluxes measured during WVA in oniscideans and other vapor absorbers

	Uptake flux ($\mu\text{g h}^{-1} \text{cm}^{-2} \text{Pa}^{-1}$)	SE	Uptake flux ($\mu\text{g h}^{-1} \text{Pa}^{-1}$)	SE	%M/12h	SE
<i>A. vulgare</i>	126.77	25.86	6.742	1.118	24.67	6.21
<i>C. convexus</i>	222.03	—	6.722	—	39.68	—
<i>O. asellus</i>	257.61	11.09	11.455	1.153	29.20	0.75
<i>P. dilatatus</i>	152.02	—	7.601	—	25.13	—
<i>P. scaber</i>	156.40	17.91	7.820	0.896	24.96	2.86
<i>P. spinicornis</i>	194.14	29.76	5.739	1.201	48.10	6.97
<i>Ps. prunosus</i>	126.84	30.52	3.162	0.757	33.52	6.95
<i>T. rathkei</i>	241.62	49.12	6.710	1.364	50.45	7.25
<i>L. oceanica</i>	290.54	46.25	19.71	2.733	19.34	3.62
<i>Arenivaga</i>	2.70	—	0.136	—	0.126	—
<i>Thermobia</i>	18.93	—	0.379	—	29.16	—
<i>Tenebrio</i>	33.80	—	2.10	—	6.67	—
<i>Onymacris</i>	24.70	—	2.50	—	12.68	—
<i>Liposcelis</i>	2.67	—	0.0086	—	137.69	—

See previous references for sources of data. Uptake fluxes are standardized for both absorbing surface area and vapor pressure deficit ($\mu\text{g h}^{-1} \text{cm}^{-2} \text{Pa}^{-1}$), and for vapor pressure deficit only ($\mu\text{g h}^{-1} \text{Pa}^{-1}$). They are also expressed as proportional gains in saturated air (% hydrated mass per 12 h). Standardized uptake fluxes reveal capacities for vapor absorption in the Oniscidea to be an order of magnitude higher than in other groups.

Oniscidea reveals a much lower coefficient of 0.519 indicating a relative increase in uptake flux in smaller animals. This may be achieved by a proportional enlargement of the absorbing endopods in early instars and smaller species, or by other mechanisms such as proportional changes in ventilatory patterns and rates of coupled water transport. We have no current explanation for why such a low scaling coefficient should be adaptive.

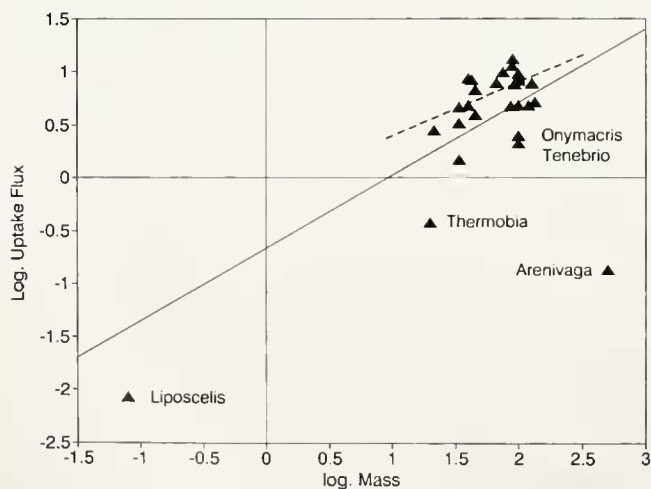


Figure 3. Log-log plot of uptake flux (in $\mu\text{g h}^{-1} \text{Pa}^{-1}$) against mass (mg) for a selection of vapor absorbers, based on the values listed in Table 3. The regression line has a slope of 0.692 indicating a scaling approximately in proportion to surface area (flux = $a \cdot \text{mass}^{0.67}$). Oniscidea, however, display a different scaling (dotted line) with a slope of 0.519. This indicates mechanisms for increasing relative uptake fluxes in smaller species. For example, proportionally larger absorbing surfaces or more efficient coupled water transport.

The relationships between standardized uptake flux and other physiological parameters reflecting water-balance efficacy are peculiar. Mean standardized uptake flux increases significantly as a function of both uptake threshold and standardized loss flux in the Crinocheta ($P < 0.02$ for both analyses; product-moment correlation). Hygic species such as *Oniscus asellus*, with high integumental permeabilities and high uptake thresholds, thus possess the most efficient uptake mechanisms. This apparently anomalous situation is considered further in the discussion.

Comparative data for passive losses, uptake fluxes and absorption thresholds permits analysis of water budgets in given nocturnal and diurnal regimes. Consider a 12-h light-dark cycle, isopods foraging nocturnally and resting in humid microhabitats diurnally in accordance with typical activity patterns (Breterton, 1957; Sutton *et al.*, 1984; Warburg *et al.*, 1984). Using pressure-standardized net uptake fluxes ($\mu\text{g h}^{-1} \text{Pa}^{-1}$), we can calculate the maximum mass of water an isopod could recover by WVA in a diurnal retreat of known ambient activity at 20°C (saturated V.P. = 2339 Pa):

$$\begin{aligned} \text{Net water-gain (mg)} &= \text{Net uptake flux (mg h}^{-1} \text{Pa}^{-1}) \\ &\times \text{absorption period (12 h)} \\ &\times [(Aa_w - \text{Threshold } a_w) \times 2339] \end{aligned}$$

Similarly, since we know loss fluxes for the same species, we can now predict the mean ambient activity in which it would incur a corresponding water debt during nocturnal foraging. It is thus possible to compile water budget curves relating ambient activities during nocturnal for-

aging to the minimum ambient activities required for diurnal replenishment of the resultant water losses. Such water budget curves are illustrated in Figure 4 for the species studied, assuming a uniform diel temperature of 20°C. The nocturnal water debt could not exceed lethal dehydration levels. Data gathered for a range of Crinocheta (5 species, cumulative n = 14) indicate a lethal dehydration level of 34.7% hydrated mass \pm 2.4% SE. The low variance and absence of outliers suggests this as a useful approximate value for the section (ca. 50% water-loss). Mean nocturnal activities in which the study species would sustain 34.7% desiccation in 12 h are listed in Table IV. For most species, these are below the minimum mean foraging a_w exploitable, given access to saturated air for diurnal WVA; that is to say, the maximum water recovered by WVA could not exceed 34.7% hydrated mass in 12 h. The magnitude of water deficits incurred during nocturnal foraging is thus limited by the capacity for replenishment by WVA, rather than short-term (nocturnal) desiccation tolerance. The major exceptions are *P. spinicornis* and *T. rathkei* in which the desiccation-limited foraging a_w exceeds the WVA-limited a_w .

The most striking revelation of this analysis is the low foraging activities which many species could exploit given even modest activities (0.94, 0.96) for diurnal WVA. With

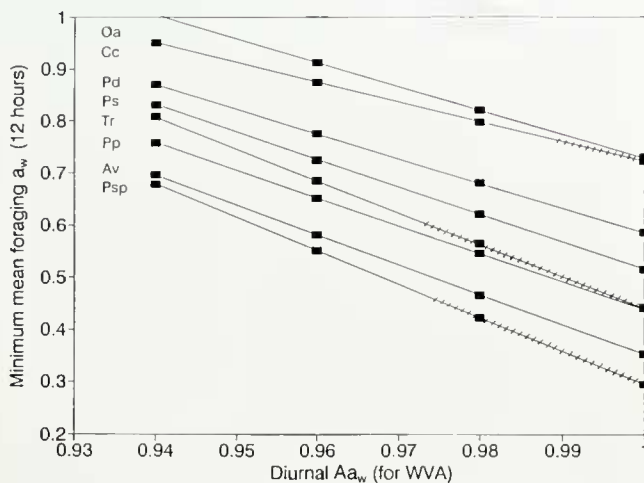


Figure 4. Plots of minimum mean ambient activities in which Crinocheta could forage nocturnally given different ambient activities for diurnal WVA. The analysis assumes a 12-h light-dark cycle. Species initials are indicated beside their respective water budget curves. For each diurnal Aa_w , the maximum attainable water-gain is calculated, knowing thresholds, uptake fluxes, and simultaneous loss fluxes for each species. The nocturnal activity in which a corresponding water-deficit would be sustained is then determined from the standardized loss fluxes. Foraging activities which would result in lethal desiccation within a 12-h period are indicated by hatched bars. All species could theoretically forage in activities below 0.75 given saturated air for diurnal WVA, and xeric species (*A. vulgare*, *P. spinicornis*, *Ps. pruinosus*) could forage in mean activities below 0.50.

Table IV

Lower lethal ambient activities for nocturnal foraging in Oniscidea at 20°C

	Aa_w (lethal)	WVA-limited foraging Aa_w
<i>A. vulgare</i>	—	0.305
<i>C. convexus</i>	0.758	0.733
<i>O. asellus</i>	0.690	0.735
<i>P. dilatatus</i>	0.404	0.589
<i>P. scaber</i>	0.322	0.517
<i>P. spinicornis</i>	0.464	0.296
<i>Ps. pruinosus</i>	0.413	0.454
<i>T. rathkei</i>	0.612	0.454
<i>L. oceanica</i>	0.657	0.811

Data were determined by: (a) the activity required to effect lethal desiccation (34.7% hydrated mass) in 12 h; (b) the activity which would result in a cumulative 12-h water loss equal to that which could be recovered by WVA in a saturated diurnal refuge over the same period.

access to a saturated diurnal refuge, all species could exploit mean foraging activities below 0.75 and maintain their long-term water budget. The curves reveal clear interspecific differences, *Porcellio spinicornis* and *Armadillidium vulgare* showing the greatest capacity to tolerate low activities, and *Oniscus asellus* and *Cylisticus convexus* requiring the highest activities. Xeric trends could be manifested primarily in either diurnal or nocturnal habitat selection. The assumptions of this analysis are considered further in the discussion.

Discussion

The comparative studies of Edney and Cloudsley-Thompson have drawn particular attention to the adaptive constraints limiting terrestrial success in the Oniscidea. These include the relatively inefficient integumental water barriers, the retention of maxillary urination and ammonotelic as the major means of nitrogenous excretion, and the need to maintain a fluid film over the pleopodal endopods for respiratory exchange. The picture emerging from these studies is that terrestrial diversification of oniscideans has primarily been the result of behavioral rather than physiological adaptations (Cloudsley-Thompson, 1956, 1974; Den Boer, 1961; Edney, 1954, 1960, 1968; Lindqvist, 1972; Little, 1983). It is perhaps appropriate to reassess this standpoint in the light of the present study.

Three main terrestrial strategies can be differentiated among the Oniscidea. An amphibious, hygrophile strategy is characteristic of the Diplocheta, generally restricted to hygric (*Ligidium*) or littoral habitats (*Ligia*). *Ligia oceanica* can tolerate indefinite periods of submersion, as well as substantial desiccation (Parry, 1953). The latter is offset,

in part, by the large size (and hence low surface area: volume ratio) and extreme osmotic tolerance. An ability to withstand haemolymph hyperosmosis up to 2000 mosmol kg⁻¹ (Parry, 1953) allows *Ligia oceanica* to attain thermodynamic equilibrium with an ambient water activity of 0.965. Provided these adaptations can maintain sub-lethal hydration levels through the 12-hourly tidal cycle, water replenishment is then available. The surprising discovery of WVA in this species provides yet another means by which it can regulate water balance. *Ligia* frequently inhabits splash-zone and supra-littoral habitats (Harding and Sutton, 1985) where water supplies are restricted to spray or pools flushed only by spring tides. As such, it may face severe salt-loading and dangers of hyperosmosis. Vapor absorption in littoral and supra-littoral habitats may serve primarily to provide a salt-free water source for osmoregulatory purposes rather than providing a source of water *per se*. This suggests a possible evolutionary scenario, with the pleon initially serving in active salt secretion in salt-loaded littoral species. Hyperosmotic NaCl in pleon fluids would constitute a preadaptation for colligative WVA, allowing animals to compensate for evaporative concentration of body fluids as well as dietary salt-loading. This would then confer obvious preadaptive benefits for the colonization of terrestrial habitats where liquid water supplies are absent or infrequent. Such a scenario is compatible with the known capacity for certain *Ligia* spp. to hyporegulate (Wilson, 1970), demonstrations of high ATPase activity and ion-transport activity by the pleopodal endopods of oniscideans (Dr. C. W. Holliday, pers. comm.; Wright *et al.*, unpub. data), and several lines of evidence suggesting a marine ancestry for the Oniscidea and the ancestral status of the Diplocheta with respect to Crinocheta (Vandel, 1943, 1965; Edney, 1968; Little, 1983; Hoese, 1981, 1982, 1984). It would be interesting to obtain data for WVA and osmoregulation in more terrestrial Diplocheta such as *Ligidium hypnorum* (Cuvier) where close convergence with the Crinocheta might be expected. The occurrence of WVA in both Diplocheta and Crinocheta, but not in Synocheta, concurs with Vandel's (1960, 1965) classification, uniting the former sections in the Ligian series, separate from the Trichoniscian (containing Synocheta) and Tylian series. However, further studies are required to determine whether WVA is an ancestral or derived condition within the Diplocheta.

The Synocheta employ a cryptozoic or 'endogean' strategy, seldom foraging in the open (Harding and Sutton, 1985; Sutton *et al.*, 1984). These species follow high ambient activities by vertical migration, avoiding desiccation behaviorally (Sutton *et al.*, 1984). Physiological adaptations to desiccating conditions are poorly developed. Cuticle permeabilities of the three species monitored in the present study are similar to or somewhat higher than those of *Ligia oceanica*. Combined with the animals' unfavor-

able surface area/volume ratios, these result in proportional loss fluxes of approximately 50% hydrated mass h⁻¹ a_w⁻¹, equating with lethal desiccation times of approximately 7 h in 90% RH, and within 1 h in humidities below 30% RH. Nano-osmometric studies (J. C. Wright, unpub. data) indicate haemolymph osmolalities for *Trichoniscus pusillus* to be in the order of 680 mosmol kg⁻¹. Even on the assumption that dehydration is accompanied by osmotic tolerance rather than haemolymph osmoregulation, this would only induce hyperosmosis to 1.36 osmol kg⁻¹ at lethal desiccation. This represents a water activity of 0.976, which may therefore be taken to represent the minimum activity (=97.6% RH) in which *T. pusillus*, and probably other Synocheta, could maintain long-term survival. The characteristically mural/lapidary habitats of *Androniscus dentiger* (Harding and Sutton, 1985) suggest unexpectedly water-stressed diurnal microclimates for a synochete and would repay further investigation.

Only the Crinocheta display substantial independence from liquid water or high ambient activities and thereby colonize mesic-xeric biotopes. Their 'physiological strategy' involves several adaptations to reduce water losses (lowered cuticle permeability, reduction or loss of the maxillary/WS excretory avenue, substitution of respiratory pleopodal endopods with exopodal lungs) and the ability to replenish water-debts above the CEA using vapor absorption. Like *Ligia* spp., Crinocheta can therefore alternate between periods of sustained desiccation and bouts of water recovery. It is well established that activity patterns of Crinocheta are intermittent and primarily nocturnal (Cloudsley-Thompson, 1952; Brereton, 1957; Den Boer, 1961; Paris, 1963, 1965). We predict, from the high efficacy of their vapor absorption, that the Crinocheta routinely sustain large water debts during nocturnal foraging. This supposition requires confirmation from field studies but gains preliminary support from the significant activity of several species in depressed humidities (Brereton, 1957; Den Boer, 1961; Paris, 1963, 1965). Such behavior has been suggested to subservise in the transpiratory loss of excess water accumulated during the day (Den Boer, 1961). Den Boer measured substantial diurnal water gains in *P. scaber* in aspen woods, though he assumed these were attributable to passive, not active absorption. This possibility can be dismissed since, for an isopod with a hydrated haemolymph water activity of 0.988, the activity gradient for integumental water gain in a saturated diurnal microclimate (A_w = 1) is only 0.012 (28.0 Pa at 20°C) and would only induce a minuscule inward water flux of 30–80 μg h⁻¹ (ca. 0.1% body mass h⁻¹) for calculated integumental permeabilities of the study species. Waterlogged habitats, on the other hand, present a serious danger to isopods owing to the hydrophilic ventral cuticle and permeable pleopodal endopods. Drowning has been

shown to constitute a major cause of mortality in grassland populations of *A. vulgare* (Paris, 1963). Even larger species regularly die within an hour when immersed, presumably from anoxia or from ion-loss and hypo-osmosis. The characteristic behavior of emerging onto the surface of soil and litter during precipitation is equally apparent in other permeable soil invertebrates (pulmonates, oligochaetes) and is generally regarded as an evasive response to waterlogging.

Interspecific differences in WVA thresholds, uptake fluxes, and integumental permeabilities reflect adaptive responses to differing xeric stresses. The strong positive correlation between uptake threshold and standardized loss flux reflects parallel adaptive trends in vapor absorption and permeability reduction. Low thresholds and high uptake fluxes will both increase water recovery in sub-saturated diurnal habitats. The ability of *C. convexus*, *P. spinicornis* and *T. rathkei* to recover maximum tolerable water deficits in sub-saturated diurnal activities (0.991, 0.975, and 0.983, respectively) over a 12-h period may reflect their frequently mesic-xeric diurnal habitats (Van Name, 1936; Harding and Sutton, 1985). However, the significant positive correlations between standardized uptake flux and threshold, and between standardized uptake flux and standardized loss flux, both suggest compensatory adaptive solutions to the problem of water recovery. Permeable species require higher uptake fluxes to counter their greater simultaneous losses. Similarly, species with high thresholds require greater uptake fluxes to compensate for the modest activity gradients they are able to generate. Unlike most vapor absorbers, oniscideans face water stress primarily as a result of relatively inefficient water barriers, not severely xeric habitats. Their remarkably high uptake fluxes are necessary to compensate for high simultaneous losses and relatively high thresholds.

It is clear from the present study that the traditional description of oniscideans as hygric, drought-shunning arthropods, possessing only modest adaptations for terrestriality, requires a fundamental revision in the case of the Crinocheta. By means of highly efficient water vapor absorption, they can routinely sustain large water-debts during nocturnal foraging and thereby tolerate low foraging activities for extended periods. The water budget analyses in this study, based on a 12-h light-dark diel cycle, are a conservative model for oniscideans in temperate latitudes since species are typically quiescent between the September and March equinoxes and are restricted to correspondingly shorter foraging periods. This means that water-debts will be more modest, and periods available for WVA will be more extensive. In addition, the analysis excludes interventions of pressure cycling in lower humidities which, though generally infrequent, can greatly boost uptake fluxes (Wright and Machin, 1993). Behavioral adaptations to limit desiccation are likely to be of

minor significance during foraging outings, particularly if these occupy restricted periods during the night (Den Boer, 1961). However, orienting kineses to temperature and humidity, as well as thigmokinesis, will serve a critical role in the selection of diurnal microhabitats compatible with WVA. Although uptake fluxes are likely to increase with temperature, WVA being an energy-dependent process (Machin, 1979a), and passive transpiration in *P. laevis* has been shown to increase linearly with ambient temperature over a biological range (Hadley and Quinlan, 1984), there is currently insufficient data available to allow predictions of the effect of temperature on the overall water budget. Excessive water vapor pressure deficits associated with diurnal temperatures may constitute the major selection pressure restricting Crinocheta to a predominantly nocturnal habit.

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